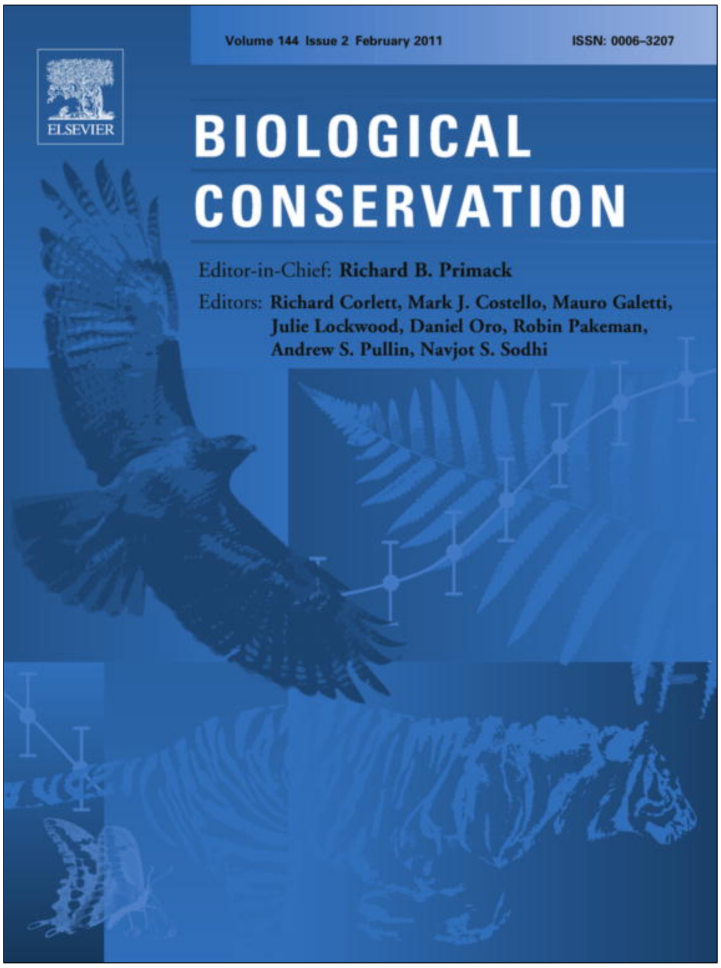
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Review

How successful are plant species reintroductions?

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ABSTRACT

Reintroduction of native species has become increasingly important in conservation worldwide for recovery of rare species and restoration purposes. However, few studies have reported the outcome of reintroduction efforts in plant species. Using data from the literature combined with a questionnaire survey, this paper analyses 249 plant species reintroductions worldwide by assessing the methods used and the results obtained from these reintroduction experiments. The objectives were: (1) to examine how successful plant species reintroductions have been so far in establishing or significantly augmenting viable, self-sustaining populations in nature; (2) to determine the conditions under which we might expect plant species reintroductions to be most successful; (3) to make the results of this survey available for future plant reintroduction trials. Results indicate that survival, flowering and fruiting rates of reintroduced plants are generally quite low (on average 52%, 19% and 16%, respectively). Furthermore, our results show a success rate decline in individual experiments with time. Survival rates reported in the literature are also much higher (78% on average) than those mentioned by survey participants (33% on average). We identified various parameters that positively influence plant reintroduction outcomes, e.g., working in protected sites, using seedlings, increasing the number of reintroduced individuals, mixing material from diverse populations, using transplants from stable source populations, site preparation or management effort and knowledge of the genetic variation of the target species. This study also revealed shortcomings of common experimental designs that greatly limit the interpretation of plant reintroduction studies: (1) insufficient monitoring following reintroduction (usually ceasing after 4 years); (2) inadequate documentation, which is especially acute for reintroductions that are regarded as failures; (3) lack of understanding of the underlying reasons for decline in existing plant populations; (4) overly optimistic evaluation of success based on short-term results; and (5) poorly defined success criteria for reintroduction projects. We therefore conclude that the value of plant reintroductions as a conservation tool could be improved by: (1) an increased focus on species biology; (2) using a higher number of transplants (preferring seedlings rather than seeds); (3) taking better account of seed production and recruitment

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when assessing the success of reintroductions; (4) a consistent long-term monitoring after reintroduction.

Contents

1. Introduction

Wild plants are under increasing threat throughout the world. Humans may have accelerated the rate of extinction by 100- to 1000-times the natural rate (Ricketts et al., 2005; Thuiller, 2007). The best place to conserve plant biodiversity is in the wild, where a large number of species present in viable populations can persist in their natural habitats with their associated ecological interactions (Mc Naughton, 1989). However, degraded and altered habitats have become a major portion of the landscape mosaic (Vitt and Havens, 2004). For the foreseeable future, accelerating demands for natural resources will continue to degrade habitat and push an increasing number of plants towards extinction (Havens et al., 2006). Habitat restoration is a good conservation approach that may allow many plant populations to recover without the use of introduced propagules (Menges, 2008). However, as many plants have transient seed banks (Thompson et al., 1997), and many are dispersal-limited (Clark et al., 2007), spontaneous recovery of rare plant populations in restored sites may be constrained by the absence of naturally occurring propagules. In this case, the reintroduction of individual plants in the wild is an essential measure to conserve threatened species (Akeroyd and Wyse Jackson, 1995). The basic biological purpose of reintroductions is establishing new or augmenting existing populations in order to increase a species' survival prospects (Pavlik, 1996; van Groenendael et al., 1998; Luijten et al., 2002).

Reintroduction of native species has become increasingly important in conservation worldwide (e.g., Maunder, 1992; Hodder and Bullock, 1997; Rout et al., 2009). The value of species reintroduction has been increasingly acknowledged in international treaties and legislation, including the Convention on Biological Diversity, the Bern Convention, the Global Strategy for Plant Conservation, the European Strategy for Plant Conservation, the Gran Canaria Declaration on Climate Change and Plant Conservation, and the European "Habitat" Directive 92/43/EEC. These agreements increase public acceptance of reintroduction efforts as an integral component of biodiversity conservation. As a result, many reintroduction efforts have been initiated. In the last 10 years the European Union consistently supported reintroductions through specific projects approved under the LIFE programme (http://ec.europa.eu/environment/life/index.htm). However, with few exceptions, there has been little effort to report reintroduction protocols and outcome. Only a few studies have reported reintroduction trials in plant species (Bottin et al., 2007). Furthermore, case studies, best practices and experiences of reintroduction most often remain in the grey literature, rather than published in the scientific literature (Hodder and Bullock, 1997; Fischer and Lindenmayer, 2000). Moreover, published literature suffers from a bias towards positive results (Deredec and Courchamp, 2007). The lack of adequate documentation may therefore be especially acute for reintroductions that are regarded as failures (Griffith et al., 1989). In reviewing the grey literature we found that reintroduction projects exist for at least 234 plant species in Europe. This information was compiled from various sources, e.g. the IUCN Reintroduction Practitioners Directory (Soorae and Seddon, 1998), the ENSCONET Database (enscobase.maich.gr) and the Italian Botanical Society Database (www.societabotanicaitaliana.it). However, the existence of different databases does not facilitate information retrieval. Furthermore, no information is available on the techniques used or the results obtained.

Recently, Menges (2008) reviewed factors that contribute to the success of reintroduction, examining the ways reintroductions have been evaluated at various stages during the process of restoration. By answering the question "when is a reintroduction successful?" this paper is a major contribution in restoration ecology. However, Menges (2008) did not answer the question

"how successful are reintroductions?" Such work has been carried out for animal species by various authors (e.g., Griffith et al., 1989; Cade and Temple, 1995; Wolf et al., 1996; Cade, 2000; Fischer and Lindenmayer, 2000). Except for Guerrant and Kaye's (2007) review of 10 plant reintroduction projects, we are unaware of any comprehensive reviews despite an earlier call for a synthesis of data on specific reintroductions to improve overall success of these efforts (Hodder and Bullock, 1997). Indeed, many projects illustrate that various plant species seem to be particularly difficult to reintroduce (e.g. Allen, 1994; Parsons and Zedler, 1997; Helenurm, 1998; Morgan, 1999; Krauss et al., 2002). Consequently, reintroduction trials have sometimes been criticised (Fahselt, 2007). However, negative results must be viewed as an advancement of knowledge (MacNab, 1983). As reintroduction is recognised as a relatively high-risk, high-cost activity (Maunder, 1992; Gorbunov et al., 2008), disseminating the results of successful – and unsuccessful – experiments is important to provide examples and case studies that will allow development of common standards and methodologies.

This study analyzes plant species reintroduction trials worldwide by focusing on the methods used and the results obtained. Three main goals were identified. The first is to examine how successful plant reintroductions have been in establishing or significantly augmenting viable, self-sustaining populations in nature. The second is to determine the conditions required for plant reintroductions to be successful. Specifically, we test whether project type, material type, number of founder individuals, number of individuals introduced, provenance of material introduced, demographic status of source population, introduction method and field manipulations play a major role in the success of reintroductions. Our third objective is to use our results to inform future plant reintroduction efforts.

2. Material and methods

2.1. Definitions

In this study, we use the terms reintroduction, reinforcement and translocation according to Akeroyd and Wyse Jackson (1995) and IUCN (1998). Reintroduction is a general term that describes the controlled placement of plant material into a natural or managed ecological area. It has also a stricter definition, i.e., the release and management of a plant into an area in which it formerly occurred, but in which it is now extinct or believed to be extinct (also called reinstatement or reestablishment). Each time we use this term in the stricter sense, we will utilize the abbreviation s.s. Reinforcement is an effort to increase population size or diversity by adding individuals to an existing population (also called supplementation, enhancement, augmentation or restocking). Translocation is the transfer (direct transportation or transplantation) of material from one part to another of the existing range of a species. In this review, the few introductions to which we refer took place within the historic range of the species but in a site in which it has never been known to occur.

Success is defined here as the ability of the population to persist and reproduce. To assess the success of a reintroduction, we focused on the survival, flowering and fruiting rates of the reintroduced plants. Seed production and recruitment are also important metrics for measuring the success of a reintroduction, but these data were rarely available in the studies we review here.

2.2. Literature review

We reviewed the literature through a search in Thomson's online Web of Science database, using the following query: (reintroduc* OR translocat* OR outplant* OR re-establish* OR transplant* OR reinforce*) AND plant. We found 82 papers on plant reintroductions, published between 1989 and 2009. These papers were examined for suitability of inclusion in the analysis. For inclusion, an article had to give sufficient methodological details (e.g. number of individuals reintroduced, material type and provenance, demography of source population, introduction method, field manipulations) and to provide data on survival, flowering or fruiting percentages, or recruitment. Consequently, 26 papers were included in the analysis (Appendix 1), yielding 114 reintroductions involving 94 plant species. Reintroductions of the same taxon to multiple locations were considered as different case studies, because of variations in methodology or environmental factors. Each reintroduction project is indeed unique with regard to the species involved, technical approach and external circumstances in which the work is conducted (Guerrant and Kaye, 2007).

2.3. Questionnaire survey

As many data are currently unpublished or in reports with restricted access, a survey was also conducted among 473 botanic gardens, universities or conservation organisations that we knew or suspected had undertaken reintroductions without having published the results. The survey was also published in the BGCI e-bulletin sent to over 4000 recipients (http://www.bgci.org/resources/news/0586/). The survey addressed biological and technical aspects of the reintroduction programmes, e.g., source and status of the reintroduced population, cultivation and reintroduction methodology, site attributes, results of the reintroduction (Appendix 2). Forty-six institutions replied to the survey (10% feedback). Fifty-five forms were correctly completed and were included in the analysis, yielding 135 reintroductions involving 82 plant species in 11 countries. Eighty-nine percent of the returned forms covered reintroduction programmes in Europe, with the remainder (11%) covering Africa, North America and Australia. Altogether our study includes 249 reintroductions involving 172 taxa belonging to 62 families (Appendix 3).

2.4. Multivariate analyses

To identify significant predictors of reintroduction outcomes, we first conducted a Canonical Correspondence Analysis (CCA; Ter Braak and Gremmen, 1987) using Canoco 4.5 for Windows (Ter Braak and Šmilauer, 2002). In order to maximize the number of cases that could be included in the analysis, we used survival rate after 1 year and flowering and fruiting rates after 2 years (after applying an arcsine-square-root transformation) as measures of reintroduction success. This initial analysis provided a check on the unimodality of the data. Because the length of the gradient was 0.38 SD, we assumed that the response curve would be monotonic and we considered a redundancy analysis (RDA). The advantage of using RDA is that its biplot provides more quantitative information than the joint plot in CCA (Jongman et al., 2000). One explanatory variable was a quantitative variable, representing the number of individuals reintroduced. The other variables were qualitative: type of project (i.e., reintroduction s.s., translocation, reinforcement, introduction), site protection status (unprotected vs. protected, the latter being either national parks, regional parks, nature reserves or Natura 2000 sites), material type (seeds vs. seedlings), material provenance (single or multiple source populations), field manipulations (fencing vs. not fencing, removing surrounding plants vs. not removing, burning vs. not burning) and good knowledge of cause of decline/extinction and environmental characteristics.

Multivariate analyses are appropriate because the success or failure of a reintroduction is likely caused by numerous factors

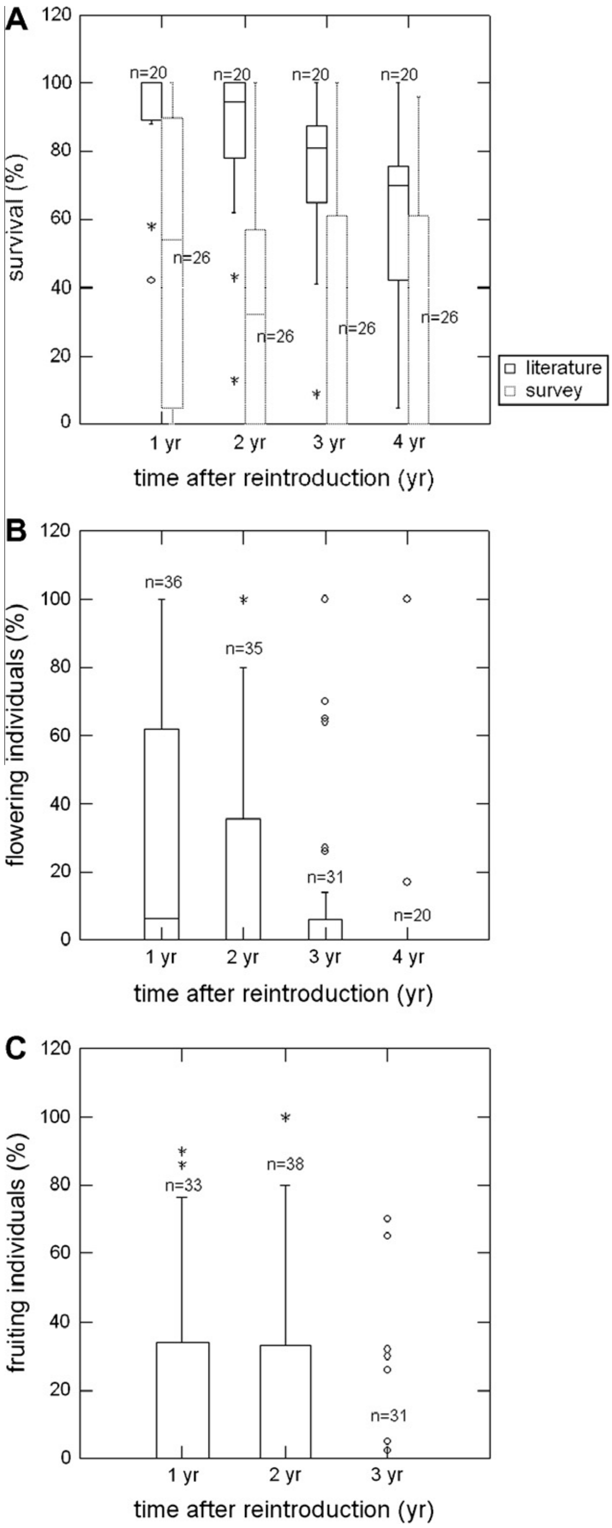

Fig. 1. Success parameters of reintroductions over time. (A) Survival percentage, showing literature data and survey data separately. (B) Percentage of flowering individuals. (C) Percentage of fruiting individuals. Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

(Wolf et al., 1996). This approach incorporates the effects of all variables on the responses of interest across multiple dimensions. However, it requires the availability of a dataset where information on the variables to be used is complete for all the reintroductions under consideration, which was the case for only 24 of reintroductions included in our study.

2.5. Univariate analyses

We also conducted univariate analyses because success variables (survival, flowering and fruiting rates) were not provided by all respondents (consequently these trials were not considered in our multivariate analysis) and because univariate analyses can identify factors potentially associated with reintroduction success (Wolf et al., 1996). In order to answer our first research aim, we evaluated the success of plant reintroductions by examining survival, flowering and fruiting rates plotted against time since reintroduction in years. Only years 1–4 were sufficiently represented in the dataset to be included in this analysis. Our second aim was then addressed by investigating the influence of each explanatory variable individually on the success-related variables, using Kruskal–Wallis and Mann Whitney tests using SYSTAT 8.0 (Wilkinson, 1998). Time was again plotted in the graphs in order to add a temporal dimension (years 1 and 3 were used here as they maximized the number of cases included). The 0.05 level of probability was accepted as threshold of significance throughout this work. Predictor variables were: number of founder individuals (individuals from which the material was collected), number of individuals reintroduced, type of project, site protection status, material type and provenance, demography of source population, introduction method, field manipulations, and knowledge of genetic variation. Literature data and survey data are displayed together on the graphs, unless otherwise stated.

2.6. Cause of reintroduction outcome

In addition to the biological and technical aspects of the reintroduction, we asked survey participants about their perceptions regarding the success or failure of the reintroduction, and the reason for the outcome. This allowed us to compare their perceptions

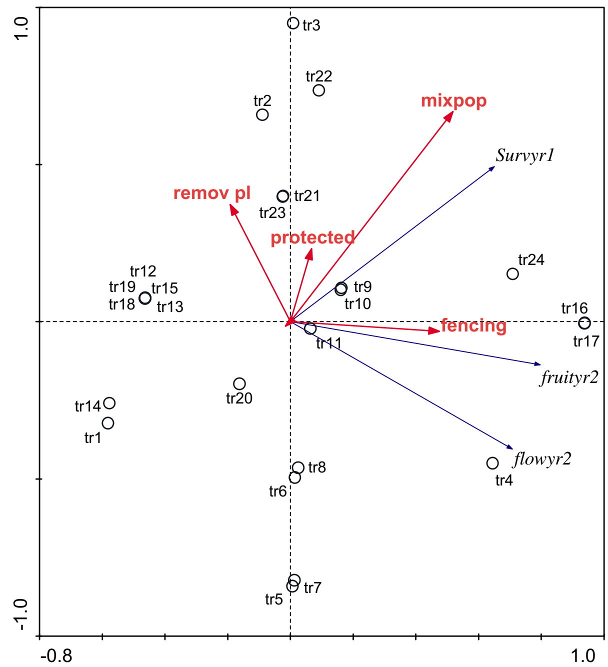

Fig. 2. RDA ordination of success-related variables (survival percentage after 1 year, flowering percentage after 2 years and fruiting percentage after 2 years) in 24 reintroduction trials. Only the variables contributing significantly to the explained variation are shown (see Table 1 for statistics on all variables). Trial position is given along axis 1 (horizontal) and axis 2 (vertical). Both axes scaled in SD-units. Vectors indicate the direction of largest change in the explanatory and success-related variables.

with their data, and to independently evaluate the reasons for failure. Such explanations are seldom recorded in the literature (Milton et al., 1999).

3. Results

3.1. Success of plant reintroductions

Overall, both the literature (Kruskal–Wallis test $H = 22.1$, $n = 80$, $P < 0.001$) and the survey data (Kruskal–Wallis test $H = 10.8$, $n = 104$, $P = 0.013$) show a significant downward trend over time in the survival of reintroduced plants (Fig. 1A). However, survival rates reported in the literature are remarkably higher than those mentioned by survey participants (Mann Whitney test: $U = 6854.0$, $n = 184$, $P < 0.001$). The percentages of flowering (Kruskal–Wallis test $H = 13.0$, $n = 122$, $P = 0.005$) and fruiting (Kruskal–Wallis test $H = 5.0$, $n = 102$, $P = 0.08$) individuals also show a decreasing trend over time since reintroduction (Fig. 1B and C), although results are only significant for the former.

3.2. Variables associated with success

The arrangement of the 24 trials in the RDA ordination is shown in Fig. 2. Eigenvalues of first and second axis were 0.498 and 0.166, respectively. Table 1 shows the variance explained by each of the variables tested and the cumulative variance explained (69%). Only three variables explained significant amounts of variation in reintroduction success: material provenance (mixpop; 21%), removing surrounding plants (remov pl; 16%) and site protection (protected; 12%). Fencing the target area explained 6% of the reintroduction success, but was only marginally significant ($P = 0.06$).

By examining each variable separately, we can confirm that reintroducing a species in protected areas significantly increases survival rate compared with reintroduction into unprotected areas (Fig. 3A; Mann Whitney test: $U = 693.0$, $n = 64$, $P = 0.012$ after 1 year; $U = 433.0$, $n = 47$, $P < 0.001$ after 3 years). Interestingly, differences become even greater after 3 years. Reintroductions s.s., reinforcements and translocations resulted in somewhat similar survival rates, significantly higher than those for introductions, especially after 3 years when it appeared that all introduced plants had died (Fig. 3B; Kruskal–Wallis test: $H = 8.9$, $n = 99$, $P = 0.030$ after 1 year; $H = 16.4$, $n = 51$, $P = 0.001$ after 3 years). Use of seedlings provided higher survival rates than use of seeds, although results were only significant in the first year after reintroduction (Fig. 3C; Mann Whitney test: $U = 537.0$, $n = 86$, $P = 0.007$ after 1 year; $U = 81.5$, $n = 40$, $P = 0.662$ after 3 years).

Table 1
Percentage variation in reintroduction success explained by explanatory variables and level of significance (Monte Carlo test, 999 permutations). Only 24 trials could be included in this analysis.

Explanatory variable	Variance explained by single variable (%)	Cumulative variance explained (%)	P-level
Plants from diverse source populations	21	21	0.007
Knowledge of cause of decline/extinction	9	30	0.096
Reducing competition by removing surrounding plants	16	46	0.008
Protected area	12	58	0.005
Fencing of the reintroduction area	6	64	0.061
Knowledge of environmental characteristics	2	66	0.310
Project type: reintroduction/ reinforcement	2	68	0.498
Number of individuals reintroduced	0	68	0.857
Burning before reintroduction	1	69	0.672
Material type: seeds	0	69	0.859

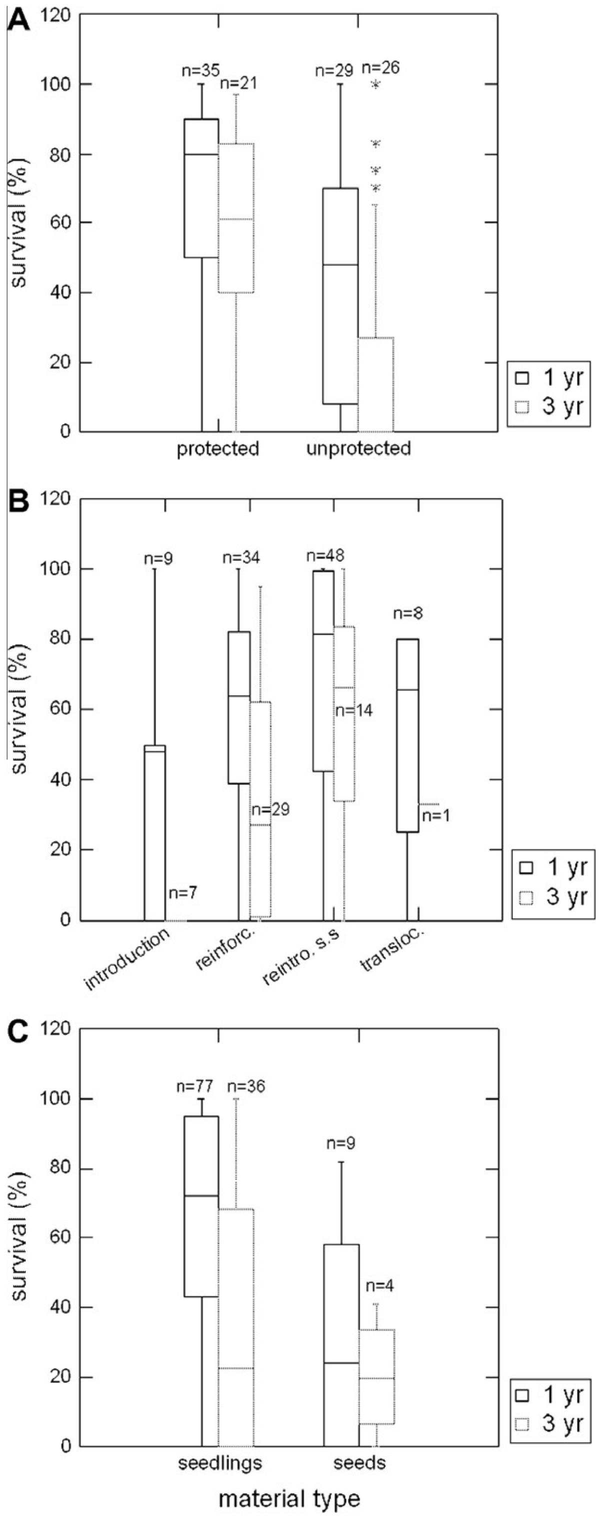

Fig. 3. Relationship between survival percentage after 1 or 3 years and (A) protection status of the reintroduction area, (B) type of project, (C) type of propagule material. Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

The number of founder individuals (individuals from which the material was collected) had no influence on the survival of the restored taxa (Fig. 4A; Kruskal–Wallis test: $H = 2.9$, $n = 58$, $P = 0.396$ after 1 year; $H = 1.8$, $n = 29$, $P = 0.611$ after 3 years), in contrast to the significant influence of the number of reintroduced individuals (Fig. 4B; Kruskal–Wallis test: $H = 14.2$, $n = 88$, $P = 0.003$ after 1 year; $H = 16.6$, $n = 45$, $P = 0.001$ after 3 years). The difference in survival rate declines over time as propagule number used increases to up to 1000 individuals (Fig. 4B).

Reintroducing a species by mixing material from diverse populations promoted a higher survival rate than using material from a single population. However, contrary to the multivariate analysis, this result was not significant in the univariate analysis (Fig. 5A; Mann Whitney test: $U = 535.5$, $n = 76$, $P = 0.401$ after 1 year; $U = 170.0$, $n = 48$, $P = 0.404$ after 3 years). Based on 3 years of data following reintroduction, we have found that using material from stable source populations (instead of decreasing ones) exhibit a positive influence on the survival rate, even if the results were significant only from the third year after reintroduction (Fig. 5B; Mann Whitney test: $U = 92.0$, $n = 44$, $P = 0.228$ after 1 year; $U = 31.0$, $n = 37$, $P = 0.010$ after 3 years).

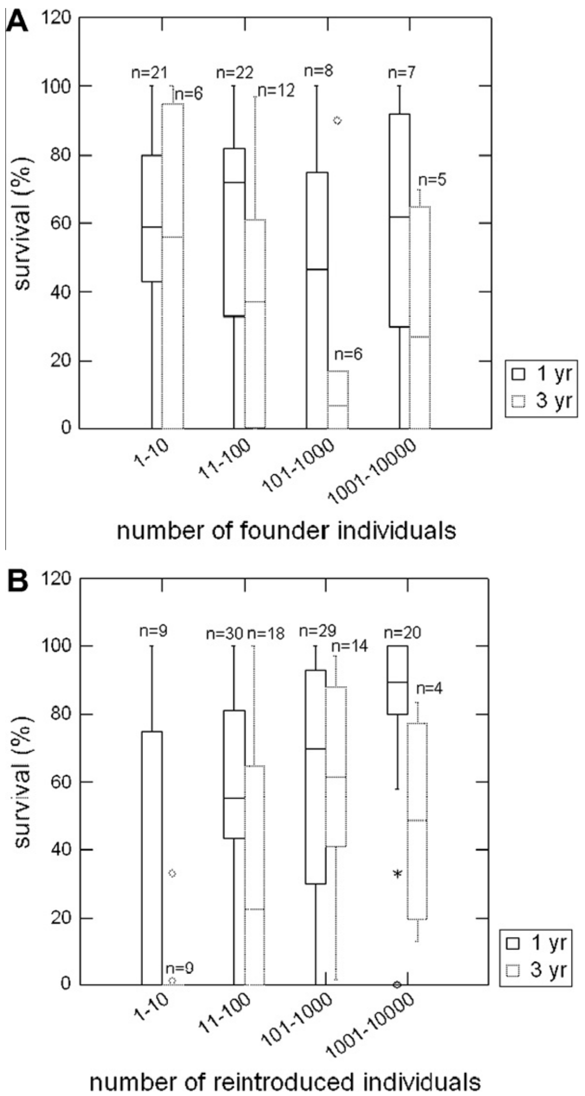

Fig. 4. Relationship between survival percentage after 1 or 3 years and (A) number of founder individuals, (B) number of individuals reintroduced. Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

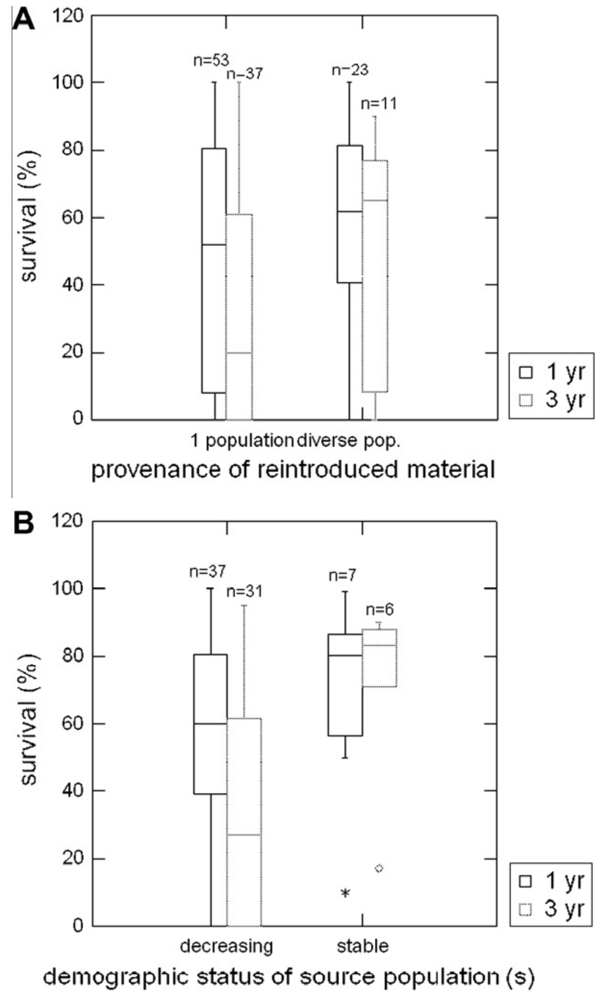

Fig. 5. Relationship between survival percentage after 1 or 3 years and (A) provenance of reintroduced material, (B) demographic status of source population(s). Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

Using bare-root seedlings resulted in a significantly higher survival rate after 3 years than when seedlings rooted in potting soil were planted (Fig. 6A; Mann Whitney test: $U = 90.0$, $n = 60$, $P = 0.513$ after 1 year; $U = 301.5$, $n = 47$, $P = 0.023$ after 3 years). Reintroduction trials accompanied by at least one site preparation or management effort (e.g., fencing, top-soil removal, nutrient enrichment, soil loosening, reducing competition by removing surrounding plants, watering, burning or protection from herbivores) resulted in significantly higher survival rates starting in the first year (Fig. 6B; Mann Whitney test: $U = 364.5$, $n = 66$, $P = 0.050$ after 1 year; $U = 185.0$, $n = 47$, $P = 0.051$ after 3 years).

Having some knowledge of the genetic variation of the target species significantly enhanced the survival rate from the first year after reintroduction, and the difference increases over time (Fig. 7; Mann Whitney test: $U = 225.5$, $n = 66$, $P = 0.054$ after 1 year; $U = 70.0$, $n = 47$, $P = 0.033$ after 3 years).

3.3. Perceived cause(s) of reintroduction outcome

Equal numbers of respondents (29%) reported successful and unsuccessful reintroduction trials (Fig. 8A). For programs of 10 years and over, this proportion increased substantially to 34%. Forty-two percent reported that it was too early to judge the success of their projects (after 10 years and more this proportion fell

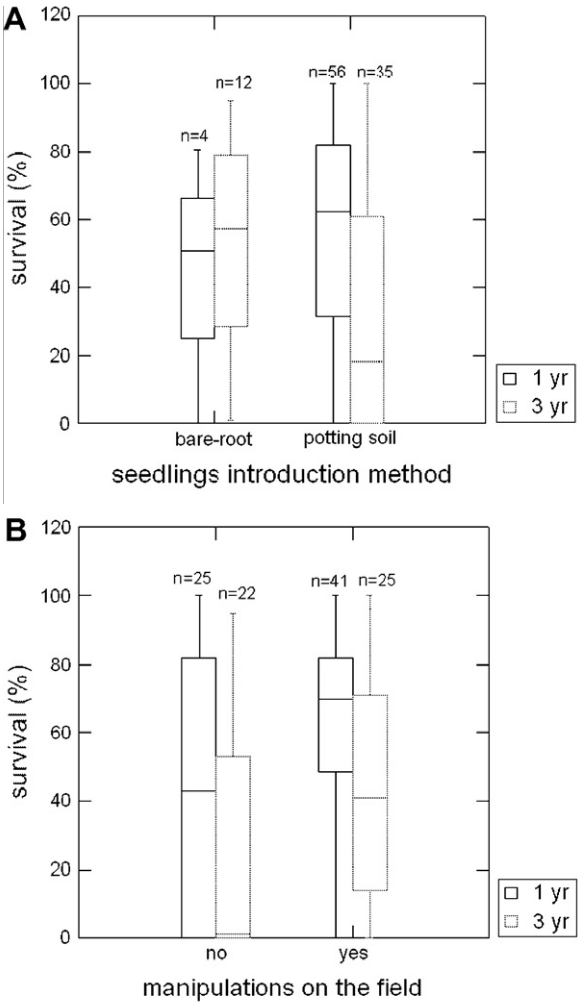

Fig. 6. Relationship between survival percentage after 1 or 3 years and (A) seedlings introduction method, (B) management of out-planting sites. Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

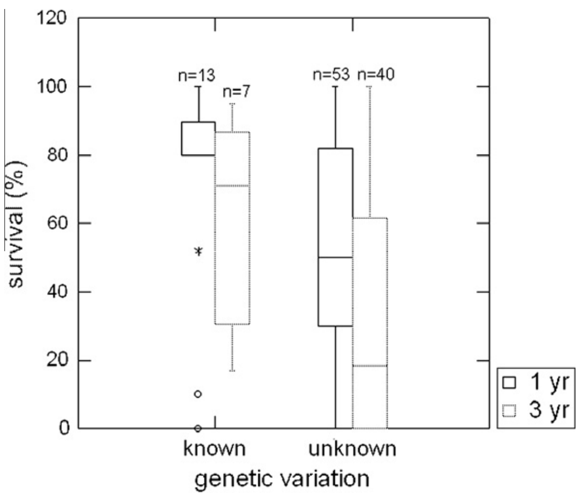

Fig. 7. Relationship between survival percentage after 1 or 3 years and knowledge of genetic variation of the reintroduced species. Outside (*) and far out values (°) are plotted as asterisks and circles, respectively.

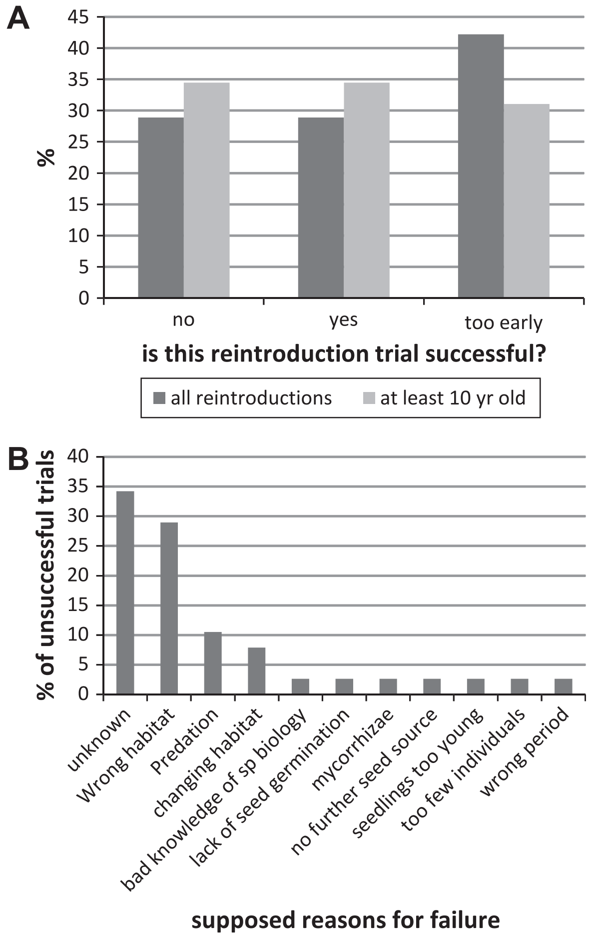

Fig. 8. (A) Distribution frequency of survey participants' perceptions regarding the success or failure of their reintroduction trials ($n = 135$). (B) Perceived causes of reintroduction failure ($n = 38$).

to 31%). The supposed reasons for failure were grouped into 11 categories (Fig. 8B). In 34% of the cases, the reason was unknown. An unsuitable habitat was the most frequently attributed reason for failure (29%). Predation (10%) and changing (degrading) habitat (8%) were also repeatedly cited as factors causing failure. Remaining causes were cited only once.

4. Discussion

4.1. Success of plant reintroductions

A key qualitative measure of the ultimate fate of reintroductions is the ability of transplants to flower and set fruit (Morgan, 2000; Tyndall and Groller, 2006; Menges, 2008). Our study reveals that survival, flowering and fruiting rates in reintroduction projects are generally quite low. Furthermore, the data indicate a downward trend with time (e.g., after 4 years, flowering percentage was only 6% on average). Few studies included data on seed production and recruitment, which would allow more direct assessment of population viability. Recruitment is considered the highest measure of success (Pavlik, 1996; Sutter, 1996), because it indicates that the population is self-sustaining through the development of successive generations (Primack, 1996). We obtained information about recruitment from the survey and from the literature for only 32% and 39% of the reintroduction attempts, respectively. In most cases, respondents reported no or only sporadic recruitment.

These data suggest that most plant reintroductions will not be successful over the long-term. However, almost one third of the survey participants categorised their project as successful. Many practitioners, therefore, may be overly optimistic in their assessments (see also Reading et al., 1997). The majority of the respondents felt it was too early to gauge success, likely concluding that 3 years may not be sufficient to indicate a long-term trend (Seddon, 1999; Guerrant and Kaye, 2007). While we agree that this timeframe is short, we were constrained by the available data. However, the declining trends in vital rates over the first few years of projects strengthens the conclusion that reintroduction is generally unlikely to be a successful conservation strategy as currently conducted.

Our results have also shown that publications are biased towards the most successful experiments. This is not surprising as many failed attempts probably remain unpublished (Berg, 1996) because negative findings are less publishable or regarded as uninteresting (Fahselt, 2007; Menges, 2008). The distorted view provided from literature review alone supports the value of the additional survey conducted. One could argue that survey results might also be biased by an over-representation of successful programs as participants in more successful programs may be more likely to respond (Reading et al., 1997). However, the significant difference between survival rates from the survey and those from the literature (two to three times higher) shows that any bias is substantially lower in the survey data.

4.2. Variables associated with success

This study has identified various parameters that seem to influence plant reintroduction outcomes. As demonstrated by our multivariate analysis and by Vergeer et al. (2005), reintroduction success is increased by using material originating from multiple populations. These authors observed that origin influenced the survival of introduced *Arnica montana* within 2 years (Vergeer et al., 2005). Multiple source populations may not be necessary if individual populations have sufficient genetic variability and may be undesirable if conservation of genetic differentiation among populations is a goal (Gordon, 1994). Where use of multiple source populations appears necessary for reintroduction success, establishment of the new composite population should be sufficiently distant from existing wild populations to preclude gene flow. Some authors have also raised concerns about outbreeding depression when using multiple source populations (Montalvo et al., 1997; Storfer, 1999; Krauss et al., 2002). Outbreeding depression is normally measured in the second and following generations (Lynch, 1991; Fenster and Galloway, 2000). As our data set included little data on seed production and recruitment, we cannot evaluate the eventual risks of outbreeding depression in the reintroductions reviewed here.

Our results also highlight a positive relationship between the number of reintroduced individuals and their survival. Demographic and genetic theories both predict that the persistence time of a population increases with its initial size (Robert et al., 2007). This prediction is consistent with findings from studies of animal (Griffith et al., 1989; Fischer and Lindenmayer, 2000) and invasive species (Lockwood et al., 2005; von Holle and Simberloff, 2005) introductions. Simulation studies have shown that demographic stochasticity is only important in populations of 50 or fewer individuals (Pollard, 1966; Menges, 1991). As 25% of the cases in our dataset reintroduced fewer than 50 individuals, demographic stochasticity may partially explain the results. Conversely, reviews by Reed and Frankham (2003) and Reed (2005) demonstrated a significant and positive relationship between population size and population fitness. The introduction of few individuals can lead to loss of genetic diversity due to inbreeding depression or post-introduction genetic drift (e.g., Barrett and Kohn, 1991; Frankham et al., 2002; Pierson et al., 2007). Consequently, smaller populations are generally less capable of adapting to novel environments, as the result of the loss of adaptive genetic variation through genetic drift (Reed et al., 2003).

While these data suggest that reintroductions should include a large number of individuals (Frankham et al., 2002), we noticed that most restoration projects include a very limited number of individuals (fewer than 100 in 43% of the cases). When considering the propagule stage, we found that the average number was 1551 (median: 830) when using seeds and 400 (median: 100) when using transplants. Small numbers are understandable because (1) reintroduction often involves rare species for which numerous propagules are not available and (2) it is a labour-intensive and costly process. Although there is danger in seeking universal levels for minimum viable population sizes (Given, 1994; Robert et al., 2007), the number of reintroduced individuals in the projects reviewed were generally substantially lower than those suggested by various authors: 500 (Given, 1994), 1000 (McGlaughlin et al., 2002), 2000 (Whitlock, 2000), 1500–2500 (Pavlik, 1996), 5000 (Reed, 2005).

The lower success rate obtained when seeds rather than seedlings were planted has previously been highlighted by various published studies (e.g. Milton et al., 1999; Drayton and Primack, 2000; Jusaitis et al., 2004; Maschinski and Duquesnel, 2006; Guerrant and Kaye, 2007; Menges, 2008). The disadvantage of using seeds to start new populations is that seeds will only rarely germinate and grow into new plants in the wild, and that the seedling stage is the most vulnerable part of the plant life-cycle (Primack and Drayton, 1997). Physically adverse environments may therefore limit the possible success with directly sown seeds. It is therefore sometimes necessary to bypass the hazards of germination in the field and use seedlings or mature plants in order to establish populations (Davy, 2002).

This study also provides some evidence that the demographic status of source populations influences reintroduction outcomes. Survival of propagules from stable source populations were up to twice the rate of those from declining populations after 3 years. As declining populations have most likely lost some rare alleles, their genetic diversity is likely to be lower than that of stable populations. Genetic diversity in the source gene pool may influence the colonising ability and prolonged persistence of a population (Polans and Allard, 1989). Diversity is also essential for the adaptability of a population (Booy et al., 2000). Although few restoration efforts include investigation of genetic diversity (see also Schemske et al., 1994), we found that survival rates of target species were much higher when genetic diversity was incorporated into the project design.

Finally, management of the out-planting site through either preparation for planting (e.g., fencing) or post-planting management (e.g., fire, reduced competition) increased the probability of reintroduction success. This focus on site management may explain the earlier result that reintroductions are more successful in protected than in unprotected sites, as management may be more probable in protected sites. Incorporation of management effort into reintroduction design may also reflect greater commitment to the reintroduction, which may also contribute to the higher success rate.

4.3. Perceived cause(s) of reintroduction outcome

The survey outcome suggests that reintroduction failure resulted from reasons predominantly intrinsic to the methodology (wrong habitat) or environmental factors (predation, changing habitat) as opposed to the biology of the introduced plants. In the literature, desiccation and herbivory are often cited as the

major factors causing mortality in reintroduction experiments (e.g., Helenurm, 1998). Concerns about habitat quality have also been raised by Vergeer et al. (2005). In their review, Bottin et al. (2007) showed that previous failures in restoration programs were mainly due to unsuitable restoration sites or the low number of plants reintroduced in the wild. Translocations involving species at risk are especially challenging because their ecological requirements are often narrower than common species (Berg, 1996; Davy, 2002). The outcome of this study illustrates the difficulty of identifying whether a habitat is (still) adequate for the target species. However, in most cases survey respondents did not investigate the reasons for failure.

Plant conservationists carrying out reintroductions often underestimate the potential importance of species biology, as shown by the partial data obtained from most survey respondents. We expect that some traits may make species good or poor candidates for reintroductions, as population persistence may depend on longevity, mating system, and dispersal ability (Picó and van Groenendael, 2007). Other plant traits that have been found to promote population persistence and spread are competitive ability, vegetative reproduction, seed bank persistence, wind pollination, plant size, growth rate and leaf area (e.g. Kolar and Lodge, 2001; Pywell et al., 2003; Farnsworth, 2007; Milbau and Stout, 2008; Cornwell and Ackerly, 2010; van Kleunen et al., 2010). In their review, Leimu et al. (2006) found a positive association between mean genetic diversity and fitness in self-incompatible but not in self-compatible species, which may be the result of a greater susceptibility to small population size in the former than in the latter (Picó and van Groenendael, 2007). Information on breeding systems is therefore essential for ex situ conservation and reintroduction programs (Weller, 1994; McKay et al., 2005). However, from the survey it appeared that the breeding system of target plants was known only for a limited number of species.

4.4. Suggestions for the design of future reintroductions

Our review suggests that propagule material type, number of individuals reintroduced, provenance of material introduced, demographic status of source population, introduction method and management of out-planting sites seem to play a key role in the success of reintroduction trials. The detection of an effect of these variables on plant reintroduction success is of considerable importance for conservation management. However, we also identified many weaknesses in reintroduction programs: (1) Insufficient monitoring following reintroduction (usually ceasing after 4 years); (2) Inadequate documentation, which is especially acute for reintroductions that are regarded as failures; (3) Lack of understanding of the underlying reasons for decline in existing plant populations; (4) Overly optimistic evaluation of success based on short-term results; and (5) Poorly defined success criteria for reintroduction projects. Clearly different practitioners have different definitions of success, which it is why it is important for introduction proposals to have explicit objectives and a monitoring plan adequate for determining if the objectives have been met.

Documenting what went wrong in reintroductions helps define the set of what could be right, and helps subsequent restoration ecologists to design more efficient efforts (Menges, 2008). According to the weaknesses we identified, we believe that the value of plant reintroductions as a conservation tool could be improved by the following:

4.4.1. Increased focus on propagule material and site protection

The success of a reintroduction remains a question of population viability involving demographic, genetic, behavioural and ecological processes (Sarrazin and Barbault, 1996). Reviews of the common practices in plant re-establishment programs have shown that reintroductions are rarely preceded by demographic and genetic studies (Hodder and Bullock, 1997; Bottin et al., 2007). While it may not be realistic to expect to have genetic data on all populations to be reintroduced, some proxies like demographic data could be used. Schemske et al. (1994) suggest that demographic criteria are far better indicators of the biological status of rare species than is information on the magnitude and distribution of genetic variation. From our survey data, it appears that reintroduced populations originate in many cases from a very small number of founder individuals (even a single founder individual in 7% of the reported experiments). In this case, reproductive failure and genetic decline in the reintroduced populations is likely to accelerate in subsequent generations (Krauss et al., 2002). Plants should also only be reintroduced from material (preferably seedlings) originating from non-decreasing populations. Therefore, the number of individuals reintroduced should be increased and based on factors like the breeding system of target species (selfing species would need fewer transplants than outcrossing species). Finally, results presented here indicate that plant species should preferably be reintroduced in an area that has legal protection status.

4.4.2. Definition of success criteria for reintroductions

Various authors have highlighted the need to define successful reintroductions of plant populations across a range of demographic and time scales (e.g., Morgan, 2000). Even if the definition of success varies among authors, it always includes the ability of a population to survive and reproduce, and to adapt to changing environmental conditions. According to the survey and literature data, it appears that more attention is paid to the survival of plants than their flowering or fruiting rates and recruitment. Many respondents to the questionnaire replied that these data were not available, not tracked, or too complex to measure. As it is clear that a newly reintroduced population that has not yet reproduced cannot be considered a success (Menges, 2008), managers should bear in mind these reproduction criteria when assessing the success of their experiments. A very precise and clear definition of success has been given by Primack and Drayton (1997): *"A* reintroduction *can be considered truly successful only when a population is expanding in numbers and area, when individuals are flowering and fruiting, when a second and third generation of plants are appearing on their own, and the population gives every indication that it will persist into future decades. Further success would involve the population dispersing seeds into the surrounding countryside and producing satellite populations*". What we seek is actually a "viable population". This trait can be assessed implementing a monitoring scheme that allows carrying out a population viability analysis (PVA).

4.4.3. Consistent long-term monitoring after reintroduction

Success criteria as recommended above obviously involve an appropriate monitoring which should not only be improved in quality but also in its time span. Long-term monitoring is necessary because initially high survival rates are often followed by reversals over time (Fahselt, 2007; Hutchings, 2010). Any reintroduction project should operate on a longer time scale than 10 years (Maunder, 1992). Some believe that monitoring to measure success is necessary for up to 25 years (Allen, 1994) or even several decades (McMahan, 1990; Milton et al., 1999; Bell et al., 2003), but these timeframes will depend on the generation time of the species involved. Similar recommendations have been suggested for animal reintroductions (Fischer and Lindenmayer, 2000).

Given the apparent low success rate of many plant reintroduction programs compared to the effort invested, we hope this paper will contribute to better design of future efforts. However, we consider the use of ex situ collections for plant species recovery only a

last resort and never a first option; the aim is to avoid ever having to reintroduce, but being able to do it if it is deemed necessary (Offord et al., 2004).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.10.003.

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